

SYSTEMATICS AND DISTRIBUTION OF CERATIOID ANGLERFISHES OF THE FAMILY MELANOCETIDAE WITH THE DESCRIPTION OF A NEW SPECIES FROM THE EASTERN NORTH PACIFIC OCEAN¹

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ABSTRACT

The ceratioid anglerfish family Melanocetidae is revised on the basis of a study of approximately 600 specimens collected from all oceans. Of the 11 nominal species of *Melanocetus* based on females, 4 are recognized: *M. johnsoni*, with *M. krechi*, *M. rotundatus*, *M. ferox*, *M. cirrifer*, and *M. megalodontis* as synonyms; *M. polyactis*; *M. niger*; and *M. murrayi*, with *M. vorax* and *M. tumidus* as synonyms. A fifth species is newly described from a single female collected from the eastern Pacific Ocean off Mazatlan, Sinaloa, Mexico. The new form differs most strikingly from its allies in having a larger esca bulb and shorter jaw teeth.

Melanocetus is widely distributed throughout all the major oceans of the world between about 250 m and some unknown lower depth limit that exceeds 3,000 m. *Melanocetus johnsoni* and *M. murrayi* are wide ranging forms, whereas *M. polyactis* and *M. niger* are apparently restricted to the eastern tropical Pacific.

Melanocetus murrayi appears to be the most phylogenetically derived member of the family. The four remaining species are much more closely related to each other than any is to *M. murrayi*. *Melanocetus johnsoni* is perhaps derived in having a relatively long illicium, and in having fewer, but longer jaw teeth. *Melanocetus polyactis* and *M. niger* are similar in having relatively short jaw teeth, a similar esca morphology, and a sympatric geographic distribution that is limited to the eastern tropical Pacific. The newly described form is derived in having an extremely large esca bulb, comparable with no other known ceratioid.

The Melanocetidae include globose, bathypelagic anglerfishes, easily separated from members of allied families by having 12 or more dorsal fin rays, 3 or 4 anal rays, and large, fanglike jaw teeth (Bertelsen 1951; Pietsch 1972a). The only recognized genus of the family was established by Günther (1864) with the description of *Melanocetus johnsoni*, based on a single female specimen collected in the Atlantic Ocean, off Madeira. Since that time, 10 additional species based on females have been described (Table 1). From a comparison of the characters used to distinguish these nominal forms, Bertelsen (1951, table 4) doubted that *M. krechi* and *M. cirrifer* could be maintained and that *M. ferox* and *M. niger* might be synonyms. *Melanocetus murrayi* and *M. johnsoni* were recognized as the only species known from the Atlantic; *M. niger*, *M. ferox*, and *M. polyactis* were considered forms restricted to the eastern tropical Pacific. Six larval

specimens from the Gulf of Panama were assigned to *M. polyactis*. The remaining larvae (approximately 600 individuals) were separated into two groups, representing *M. murrayi* and *M. johnsoni*, on the basis of geographic distribution, fin ray counts, and a comparison of larval and adolescent female pigmentation. Despite these allocations, Bertelsen (1951) made it clear that "... the separation of the species is still very uncertain and future investigations and material will probably make it necessary to revise this synopsis."

At the time of Bertelsen's (1951) monograph on the Ceratioidei, 19 metamorphosed melanocetid males were known. Of these, 14 had been set up as types of 12 separate species, and 5 were uncertainly placed. On the basis of subdermal pigment, fin ray counts, and geographic distribution, Bertelsen (1951) synonymized 6 of these 12 nominal forms with *M. johnsoni* and 4 with *M. murrayi*. The remaining two species based on males, *M. longirostris* and *M. nudus*, each differing slightly from the rest of the material, were tentatively retained (Table 1).

With the vast increase in the amount of material of *Melanocetus* made available in the last 25

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TABLE 1.—Reallocation of nominal forms of *Melanocetus*. Valid names on right. Synonymy for species based on males after Bertelsen 1951.

Females:		
<i>Melanocetus johnsoni</i> Gunther 1864	}	<i>Melanocetus johnsoni</i> Gunther 1864
<i>Melanocetus krechii</i> Brauer 1902		
<i>Melanocetus rolundatus</i> Gilchrist 1903		
<i>Melanocetus ferox</i> Regan 1926		
<i>Melanocetus cirrifer</i> Regan and Trewavas 1932		
<i>Melanocetus megalodontis</i> Beebe and Crane 1947	}	<i>Melanocetus polyactis</i> Regan 1925
<i>Melanocetus polyactis</i> Regan 1925		
<i>Melanocetus niger</i> Regan 1925 (in part)		
<i>Melanocetus niger</i> Regan 1925 (in part)	}	<i>Melanocetus niger</i> 1925
<i>Melanocetus murrayi</i> Gunther 1887		
<i>Melanocetus vorax</i> Brauer 1902	}	<i>Melanocetus murrayi</i> Gunther 1887
<i>Melanocetus tumidus</i> Parr 1927		
Males:		
<i>Centroceretus spinulosus</i> Regan and Trewavas 1932	}	<i>Melanocetus johnsoni</i> Gunther 1864
<i>Xenoceratias micracanthus</i> Regan and Trewavas 1932		
<i>Xenoceratias heterorhynchus</i> Regan and Trewavas 1932		
<i>Xenoceratias laevis</i> Regan and Trewavas 1932		
<i>Xenoceratias brevirostris</i> Regan and Trewavas 1932		
<i>Xenoceratias braueri</i> Koeloe 1944	}	<i>Melanocetus polyactis</i> Regan 1925
<i>Rhynchoceratias rostratus</i> Regan 1926 (in part)		
<i>Rhynchoceratias leucorhinus</i> Regan 1926 (in part)		
<i>Rhynchoceratias acanthrostris</i> Parr 1927	}	<i>Melanocetus murrayi</i> Gunther 1887
<i>Rhynchoceratias latrinus</i> Parr 1927		
<i>Rhynchoceratias longipinnis</i> Parr 1930		
<i>Xenoceratias regani</i> Koeloe 1944		

yr, we are able to recognize five species based on females. Four of these are previously described forms: *M. johnsoni*, represented by 346 specimens collected from all three major oceans of the world; *M. polyactis* and *M. niger*, known from 15 and 6 specimens both restricted to the eastern tropical Pacific; and *M. murrayi*, 140 specimens of worldwide distribution. The fifth is a new species recently collected by the *Velero IV* of the University of Southern California in the eastern Pacific off Mazatlán, Sinaloa, Mexico. It differs strikingly from its allies in having a considerably larger esca bulb and shorter jaw teeth.

Although the number of known male specimens has increased nearly fourfold since Bertelsen's (1951) work, no new diagnostic data are available. We have examined 73 individuals (11.5–24 mm standard length), none of which can be satisfactorily identified to species based on females. As predicted by Bertelsen (1951), the variation in the number of denticular teeth is greater than previously thought and values given in his key overlap to a much greater extent than is indicated. An attempt to utilize differences in larval pigmentation, thought to be more or less retained, at least in the younger metamorphosed males, failed to separate the material into groups that could be associated with species based on females. Although Bertelsen's (1951) synonymies for nominal species based on males are retained here, additional male specimens are listed as *Melanocetus* sp.

METHODS AND MATERIALS

Standard lengths (SL) are used throughout unless otherwise stated. Measurements were taken from the left side whenever possible and rounded to the nearest 0.5 mm. To ensure accurate fin ray counts, skin was removed from the pectoral fins and incisions were made to reveal the rays of the dorsal and anal fins. Sockets, indicating missing teeth in the jaws and on the vomer, were included in total tooth counts. Jaw tooth counts are the sum of both right and left sides. Head depth is the distance from the tip of the sphenotic spine to the base of the quadrate spine. Head width is the distance between the anterolateralmost margins of the sphenotic bones. Lower jaw length is the distance from the symphyseal spine to the posterior-most margin of the articular. Illicium length is the distance from the articulation of the pterygiophore of the illicium and the illicial bone to the distal surface of the esca, excluding esca appendages. The width of the pectoral fin lobe is the distance between the point of articulation of the uppermost fin ray to the articulation of the lowermost fin ray. Terminology used in describing the various parts of the angling apparatus follows Bradbury (1967). Definitions of terms used for the different stages of development follow Bertelsen (1951). Complete locality data are given for primary type material only.

The comparative osteological investigation was

based primarily on five female specimens (two *M. murrayi*, 75 and 84 mm SL, and three *M. johnsoni*, 44.5, 60, and 75 mm SL; material representing the remaining species of the genus was unavailable) cleared and stained with Alizarin red S following the trypsin digestion technique (Taylor 1967). Bone terminology follows Pietsch (1974).

Unless otherwise indicated, all diagnoses and descriptions are based on female specimens >20 mm SL. For males and larvae see Bertelsen (1951). Material is catalogued in the following institutions: Australian Museum, Sydney (AMS); British Museum (Natural History), London (BMNH); Bingham Oceanographic Collections, Peabody Museum of Natural History, Yale University (BOC); California Academy of Sciences, San Francisco (CAS); Florida State Museum, University of Florida, Gainesville (FSM); Institute of Oceanology, Academy of Sciences, U.S.S.R., Moscow (IOAN); Institute of Oceanographic Sciences, Surrey, England (IOS); Institut für Seefischerei, Hamburg (ISH); Natural History Museum of Los Angeles County (LACM); Museum of Comparative Zoology, Harvard University (MCZ); National Museum of New Zealand, Wellington (NMNZ);

Royal Ontario Museum, Toronto (ROM); South African Museum, Cape Town (SAM); University of Bergen, Zoological Museum (UBZM); University of Miami Marine Laboratory, (UMML); National Museum of Natural History, Washington, D.C. (USNM); Virginia Institute of Marine Science, Gloucester Point (VIMS); Zoological Museum, Humboldt University, Berlin (ZMHU); Zoological Museum, University of Copenhagen (ZMUC).

OSTEOLOGY OF FEMALES

The osteology of *Melanocetus* was partially described by Regan (1926, fig. 10), Parr (1930a, fig. 2-5, male only), Regan and Trewavas (1932, fig. 19-28), and Bertelsen (1951, fig. 13, 14). In the following account, only those comparative aspects that need amending or that have not previously appeared in the literature are discussed.

Cranium (Figures 1-9). — The anterior portion of the cranium of *Melanocetus* is considerably wider, relative to the posterior portion, than in other ceratioids; the distance between the lateral margins of the ethmoid cartilage is nearly equal to the

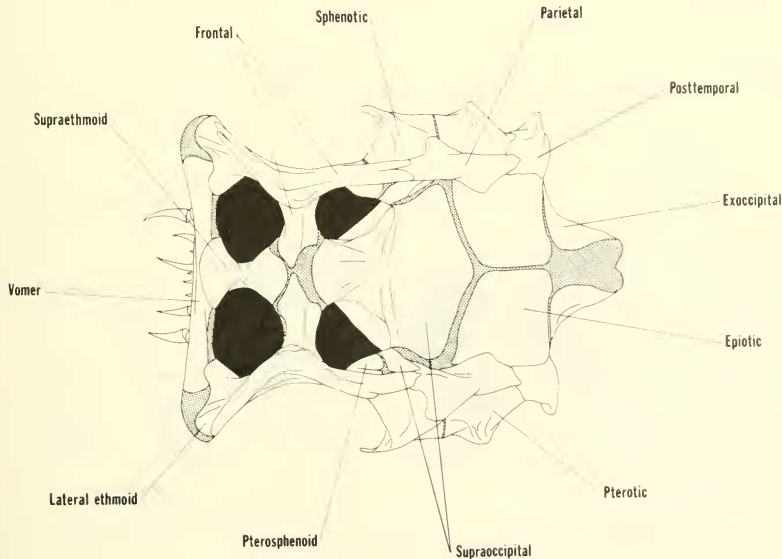


FIGURE 1.—Dorsal view of cranium of *Melanocetus johnsoni*, LACM 32786-1, 75 mm SL. Cartilage stippled, open spaces solid black.

distance between the tips of the sphenotic bones (Figures 1, 2) The head of the vomer, bearing as many as 10 recurved teeth, is also unusually wide (Figures 1, 2, 5-7). The frontals are triradiate in shape and widely separated from each other along their dorsal margins, approaching one another on

the midline only at their ventromedial extensions. A semicircular-shaped pterospheonoid is present under the posterior extension of each frontal. The parasphenoid is well separated from the ventromedial extensions of the frontals. Posteromedially, the parasphenoid underlies the anterior

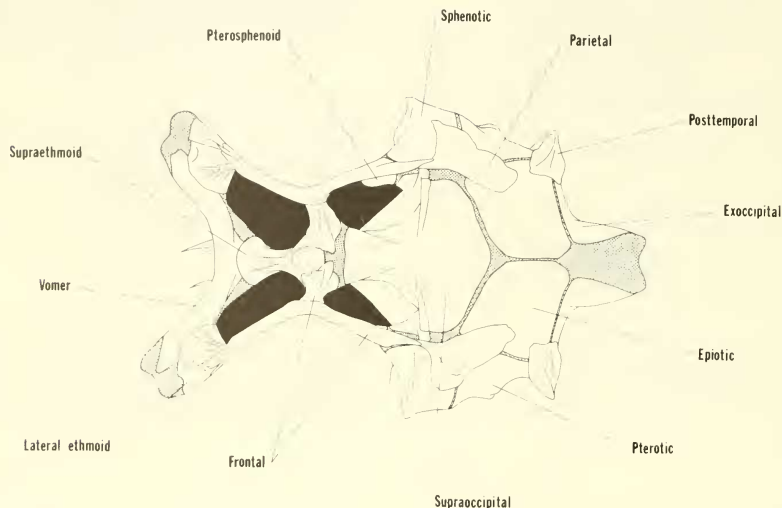


FIGURE 2.—Dorsal view of cranium of *Melanocetus murrayi*, LACM 31501-3, 84 mm SL. Cartilage stippled, open spaces solid black.

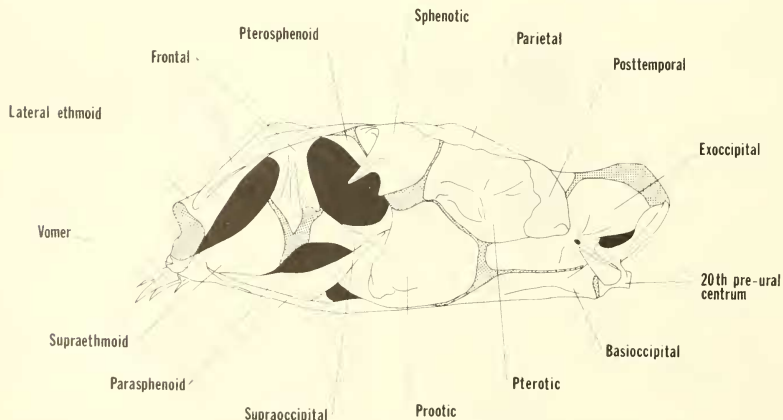


FIGURE 3.—Lateral view of cranium of *Melanocetus johnsoni*, LACM 32786-1, 75 mm SL. Cartilage stippled, open spaces solid black.

projection of the supraoccipital; posteriorly directed dorsolateral extensions of the parasphenoid make contact laterally with the respective prootic (Figures 3, 4).

The large prootics are separated from each other anteriorly by the anterior process of the supraoccipital. Ventrally, each prootic forms a relatively large, anterolaterally directed, conical pro-

jection not found in other ceratioids (Figures 3-5, 8).

The supraoccipital is the largest element of the cranium, making up a considerable portion of the roof of the cranium. Together with the frontals, the supraoccipital forms the floor of a deep, V-shaped illicial trough (Figure 8). An anteriorly directed extension of the supraoccipital that sep-

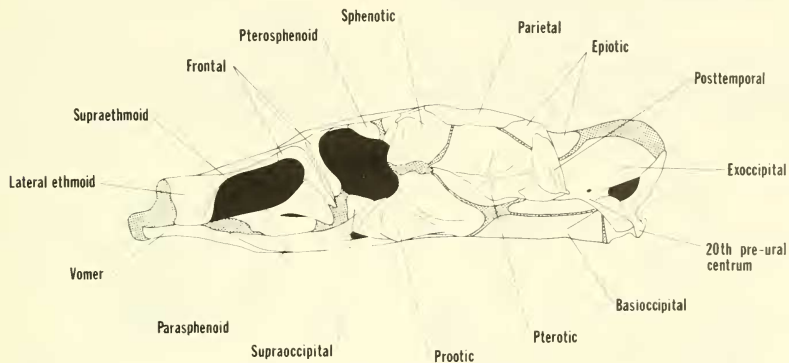


FIGURE 4.—Lateral view of cranium of *Melanocetus murrayi*, LACM 31501-3, 84 mm SL. Cartilage stippled, open spaces solid black.

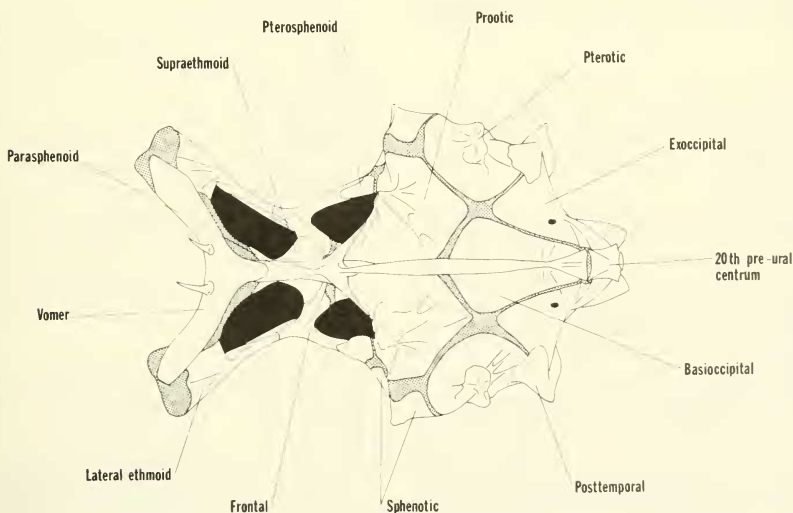


FIGURE 5.—Ventral view of cranium of *Melanocetus murrayi*, LACM 31501-3, 84 mm SL. Cartilage stippled, open spaces solid black.



FIGURE 6.—Anterior view of anterior half of cranium of *Melanocetus johnsoni*, LACM 32786-1, 75 mm SL. Cartilage stippled.

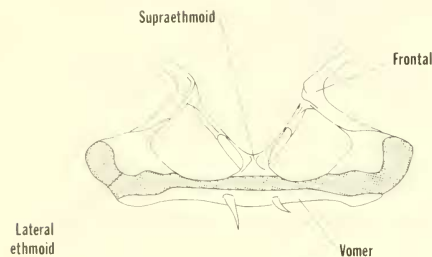


FIGURE 7.—Anterior view of anterior half of cranium of *Melanocetus murrayi*, LACM 31501-3, 84 mm SL. Cartilage stippled.

arates the prootics on the midline, is narrowly separated by cartilage from the ends of the ventromedial extensions of the frontals. The supraoccipital is not overlapped by the parietals (Figures 1-5).

The cranium of *M. murrayi* is considerably more elongate and compressed compared with that of its congeners (Figures 3, 4). As a consequence, the anterior margin of the vomer of *M. murrayi* is deeply concave (nearly straight in other forms), the frontals are more elongate and considerably lighter in construction, the sphenotics are much less produced forward, and the parietals do not extend posteriorly to overlap the posttemporals as they do in other *Melanocetus* species (Figures 1, 2).

Mandibular arch (Figures 10, 11).—The anterior portion of the premaxilla bears a short ascending process and a slightly longer articular process. A small (compared with those of oneirodids, Pietsch 1974) symphyseal cartilage lies just behind the

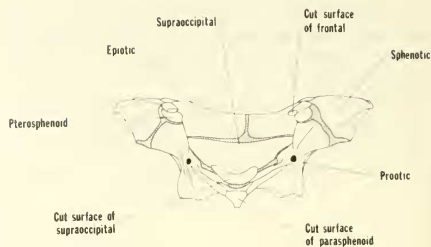


FIGURE 8.—Anterior view of posterior half of cranium of *Melanocetus murrayi*, LACM 31501-3, 84 mm SL, anterior portion removed. Cartilage stippled.

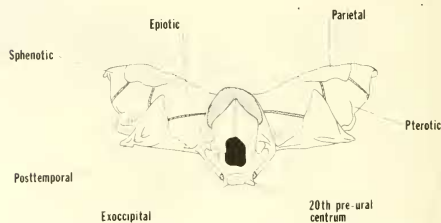


FIGURE 9.—Posterior view of cranium of *Melanocetus murrayi*, LACM 31501-3, 84 mm SL. Cartilage stippled.

posteriorly notched symphysis of the premaxillae. There is no postmaxillary process of the premaxilla. The elongate portion of each premaxilla may bear up to 89 recurved, depressible teeth of mixed sizes (Figure 10).

On each side, the posterior ends of the premaxilla and maxilla are united by connective tissue to each other and to the lateral surface of the ascending process of the articular of the lower jaw, preventing any forward rotation of the upper jaw bones to close off the corners of the mouth. There is no elongate, anterior maxillomandibular ligament originating on the dentary as in oneirodids (labial cartilage of Le Danois 1964; Pietsch 1972a, 1974).

The dentaries meet on the midline to form a strong symphyseal spine. Each dentary may bear up to 71 recurved, depressible teeth of mixed sizes (Figure 11).

Palatine and hyoid arches (Figures 11, 12).—The distal portion of the palatine arch (including the mesopterygoid, ectopterygoid, and palatine) is elongate and slender throughout (Figure 11). The small mesopterygoid is in contact with the metap-

terygoid. The suspensorium is unusually narrow and elongate (due largely to the extremely narrow and elongate quadrate), and directed obliquely backward. The posterior head of the hyomandibular is the larger of the two heads forming a broad articulation with the pterotic. The interhyal is

short and relatively thick (compared with that of oneirodids, Pietsch 1974).

The hyoid apparatus (including epihyal, ceratohyal, and upper and lower hypohyals) is relatively short and thick (Figure 12). The lower hypohyal extends down beyond the ventral margin of the ceratohyal. In other ways this portion of the hyoid arch does not differ substantially from that described for oneirodids (Pietsch 1974).

Opercular apparatus (Figure 11).—The opercular apparatus is somewhat reduced (compared with that of oneirodids, Pietsch 1974). The opercle

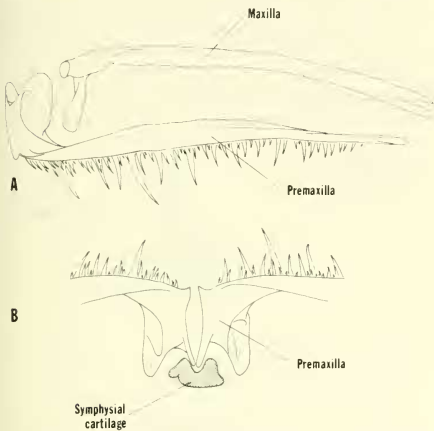


FIGURE 10.—Elements of upper jaw of *Melanocetus murrayi*, LACM 31501-3, 84 mm SL: A. Maxilla and premaxilla, left lateral view; B. Symphysis of premaxillae, dorsal view.

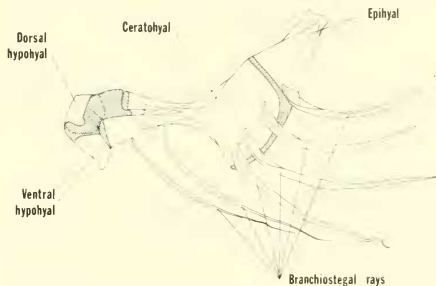


FIGURE 12.—Lateral view of hyoid apparatus of *Melanocetus murrayi*, LACM 31501-3, 84 mm SL, interhyal not shown. Cartilage stippled.

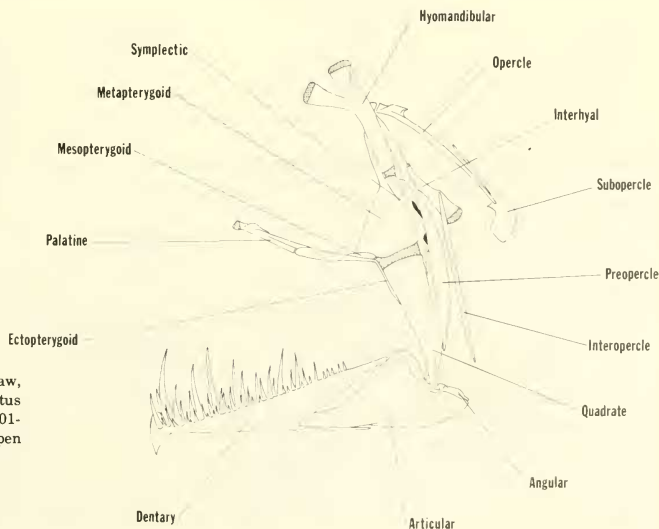


FIGURE 11.—Lateral view of lower jaw, suspensorium, and opercular apparatus of *Melanocetus murrayi*, LACM 31501-3, 84 mm SL. Cartilage stippled, open spaces solid black.

is notched posteriorly, but the upper fork of this bone is considerably shorter than the lower fork and sometimes absent. The subopercle is narrow and elongate, the upper part tapering to a fine point, the lower part rounded with a well-developed anterior spine or projection. The interopercle is unusually long and slender. The preopercle is more or less straight.

Branchial arches (Figure 13).—Pharyngobranchials I and IV are absent; those of the second and third arches are well developed, bearing four to nine recurved and depressible fangs. Epibranchial

I is reduced lying free in the connective tissue matrix. Ceratobranchial V is also reduced but tightly connected to the medial-proximal margin of ceratobranchial IV. There are three hypobranchials, and a single basibranchial ossification surrounded by a triangular-shaped cartilage.

Vertebrae and caudal skeleton (Figure 14).—The vertebral column forms a sigmoid curve, dipping down behind the region of the gut and sloping up again to support the tail. In the five cleared and stained specimens examined there are 20 vertebral centra (including the half-centrum to which is

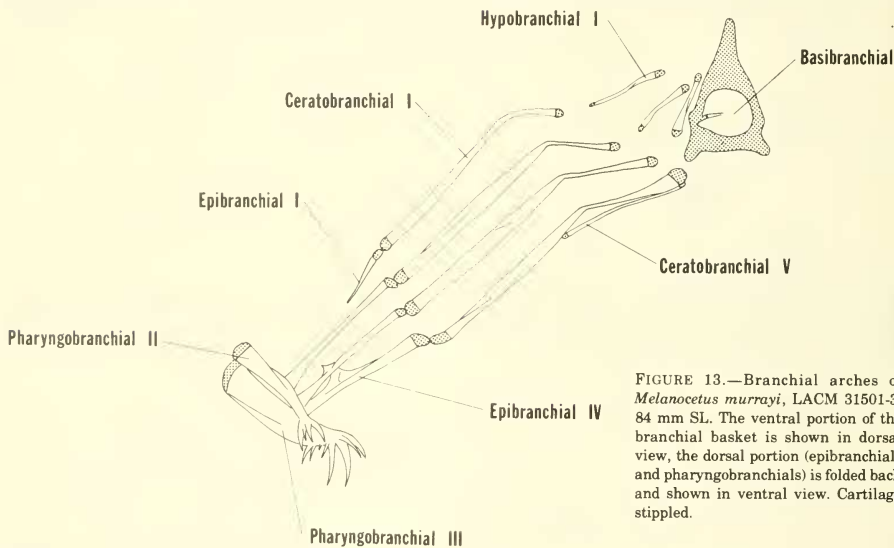


FIGURE 13.—Branchial arches of *Melanocetus murrayi*, LACM 31501-3, 84 mm SL. The ventral portion of the branchial basket is shown in dorsal view, the dorsal portion (epibranchials and pharyngobranchials) is folded back and shown in ventral view. Cartilage stippled.

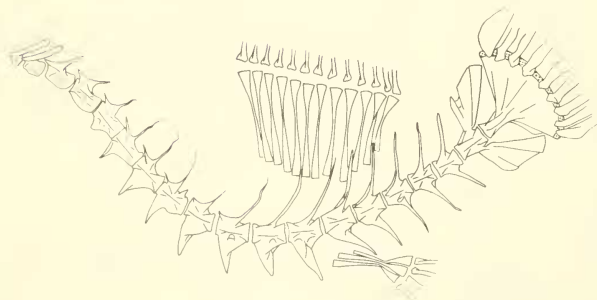


FIGURE 14.—Lateral view of vertebral column, dorsal and anal fins, and caudal skeleton of *Melanocetus murrayi*, LACM 31501-3, 84 mm SL. Cartilage stippled.

fused the hypural plate, Pietsch 1972a) of which 13-15 are caudal vertebrae (those bearing complete haemal arches). Epurals are absent. The hypural plate is unnotched posteriorly and bears the overlapping bases of nine principal caudal rays, the uppermost of which is exceptionally large. The uppermost and two lowermost caudal rays are simple, the central rays are bifurcated distally.

Median fins and illicial apparatus (Figures 14, 15).—There are 13-19 biserial, segmented, and unbranched dorsal fin rays, the number varying somewhat among species. The rays are supported by elongate, closely associated radials, usually one less than the number of rays. All species of the genus have 4 anal fin rays (of 353 specimens counted, only 2 had 3 anal rays, and only 2 had 5 rays) that are like those of the dorsal fin, invariably supported by 3 similar, closely associated radials (Table 2, Figure 14).

The pterygiophore of the illicium is strongly compressed with a thin, bladelike ventral expansion. The length of the pterygiophore varies from 17% SL in *M. murrayi* to 33% SL in *M. johnsoni*. The remnant of the second cephalic ray is a minute ossification lying on the pterygiophore just behind the articulation with the illicial bone (Figure 15). The length of the illicial bone varies slightly among *Melanocetus* species, becoming longer proportionately with growth.

Pectoral girdle, pectoral fin, and pelvic bone (Figure 16).—Each posttemporal overlaps the respective pterotic, epiotic, and exoccipital. It is in turn overlapped by the parietal in *M. johnsoni*, but widely separated from this bone in *M. murrayi*.

An ossified posteroventral process of the pectoral is absent but perhaps represented by a posteroventral cartilaginous extension. There are four pectoral radials, the lower two of which become completely fused with each other giving the appearance of only three radials (Regan and Trevas 1932, fig. 22; Pietsch 1972a).

The pectoral fin lobe of *M. murrayi* is considerably smaller than that of other *Melanocetus* species (Figure 16A). In other ways the elements of the pectoral girdle, pectoral fin, and pelvic bone do not differ substantially from those of oneirodids (Pietsch 1974).

Skin spines.—Minute dermal spines (approximately 0.03-0.1 mm long) are present in the skin

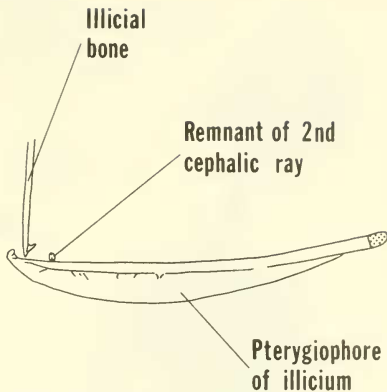


FIGURE 15.—Bones of illicial apparatus of *Melanocetus murrayi*, LACM 31501-3, 84 mm SL, left lateral view. Cartilage stippled.

of the two species examined osteologically. In *M. johnsoni* they are most numerous on the side of the trunk under the dorsal fin (where there are about 6 spines/mm²) but become progressively more widely scattered anteriorly and finally disappear in the area of the upper and lower jaws (Struhsaker 1962). In the two specimens of *M. murrayi* examined osteologically the spines are confined to the caudal peduncle.

SYSTEMATICS

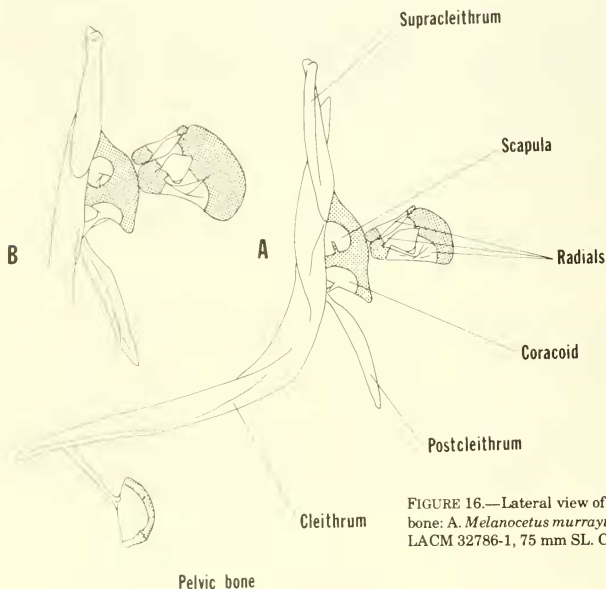
Family Melanocetidae Regan 1912

Type genus *Melanocetus* Günther 1864

Diagnosis.—The metamorphosed females of the Melanocetidae are distinguished from those of all other ceratioid families by having the following combination of characters: jaws equal anteriorly; supraethmoid present; parietals present; pterosphenoïd present; anterior maxillomandibular ligament absent (Pietsch 1972a); hyomandibular with a double head; hypohyals 2; branchiostegal rays 6; operculum bifurcate, upper fork reduced; suboperculum slender, as long as lower fork of operculum, with strong anterior spine; pharyngobranchials I and IV absent; epibranchial I reduced; a single ossified basibranchial; epibranchial and ceratobranchial teeth absent; epurals absent; only an ossified remnant of second cephalic ray present; dorsal fin rays 13-17, anal fin

TABLE 2.—Fin ray frequencies for females of *Melanocetus* species.

Species	Dorsal						Anal				Pectoral (both sides)							
	12	13	14	15	16	17	3	4	5	15	16	17	18	19	20	21	22	23
<i>Melanocetus johnsoni</i>			6	70	64	2	1	1	136	1		13	34	69	36	12	2	1
<i>Melanocetus polyactis</i>				4	4	4	2		13	1			2	3	12	4	2	1
<i>Melanocetus niger</i>				3	2				5					2	2	5	1	
<i>Melanocetus eustalus</i>						1			1			2						
<i>Melanocetus murrayi</i>	1	32	29						62		5	17	37	8	5	1		
Total	1	38	106	71	6	3	1	217	2	5	19	52	47	88	46	15	3	1

FIGURE 16.—Lateral view of pectoral girdle, pectoral radials, and pelvic bone: A. *Melanocetus murrayi*, LACM 31501-3, 84 mm SL; B. *M. johnsoni*, LACM 32786-1, 75 mm SL. Cartilage stippled.

rays 4 (rarely 3 or 5), caudal fin rays 9 (1-6-2); ossified posteroventral process of coracoid absent; pectoral radials 4, fusing to 3 with growth; pelvic bones expanded distally; esca without denticles; minute, widely spaced skin spines present in at least some species.

The metamorphosed males of the *Melanocetidae* are distinguished from those of all other ceratioid families in having the following combination of characters: free-living; jaw teeth absent; upper denticular with 2-3 semicircular series of strong, recurved denticles, fused with a median series of 3-9 enlarged dermal spines that articulate with the pterygiophore of the illicium; lower denticular with 10-23 recurved denticles, fused into a median and two lateral groups; eyes directed laterally, elliptical in shape, pupil larger than lens; olfac-

tory organs large, nostrils lateral, nasal area unpigmented, inflated; dorsal fin rays 12-16, anal fin rays 4, caudal fin rays 9 (1-6-2); skin spinulose or naked.

Description. — Females relatively short and deep, globular (but often appearing highly compressed apparently due to deformation upon capture, compare Figures 17, 18); head short; mouth large, nearly vertical, cleft not extending past eye; lower jaw with a well-developed symphyseal spine; oral valve weakly developed; two nostrils on each side on distal surface of a rounded papilla; eye small, subcutaneous, appearing through a circular, translucent area of integument within a shallow, orbital pit formed between sphenotic and frontal bones; gill opening oval in shape, situated posteri-

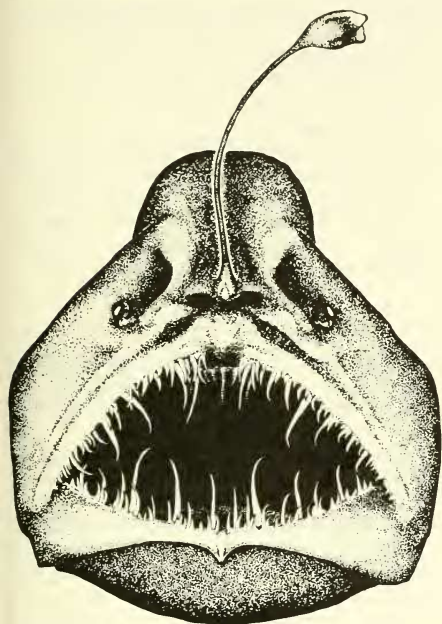


FIGURE 17.—Anterior view of *Melanocetus johnsoni*, LACM 31484-1, 85 mm SL. Drawn by Elizabeth Anne Hoxie.

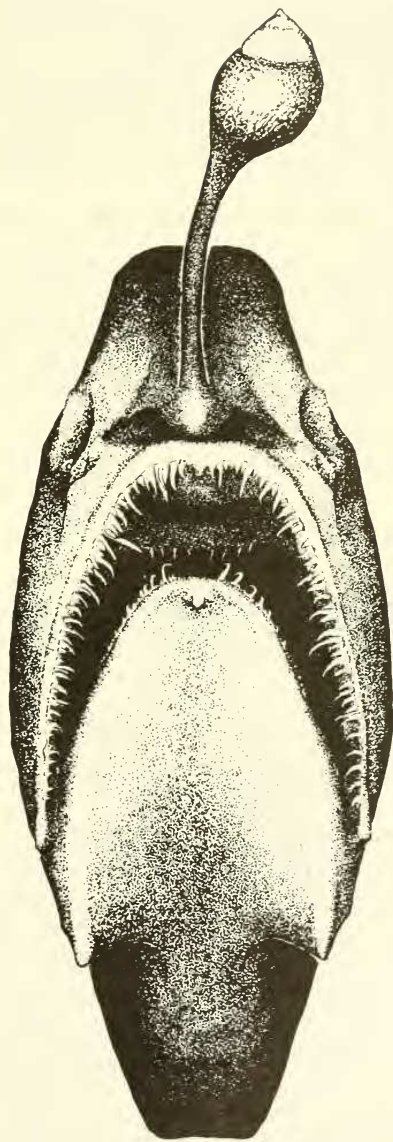


FIGURE 18.—Holotype of *Melanocetus eustalus*, LACM 30037-12, 111 mm SL, anterior view. Drawn by Elizabeth Anne Hoxie.

or to pectoral lobe; all four epibranchials closely bound together by connective tissue; anterior half of ceratobranchial I bound to medial surface of ceratohyal by connective tissue, posterior half free; gill filaments present on anteriormost tip of ceratobranchial I and full length of ceratobranchials II through IV; pseudobranch absent; no opening behind fourth gill arch; ovaries paired; pyloric caeca absent.

Illicial length 23.1-60.8% SL; anteriormost tip of pterygiophore of illicium exposed, emerging on snout between eyes, its posterior end concealed under skin; escal bulb simple, usually with a rounded or conical, distal prolongation, and often with posterior and anterior crests; elongate appendages and filaments absent.

Jaw teeth slender, recurved, and depressible, some slightly hooked distally, those in lower jaw less numerous, but slightly longer than those in upper jaw; number of teeth in lower jaw 32-142, in upper jaw 29-178; longest tooth in lower jaw 6.9-

25.0% SL; vomer with 0-12 teeth; pharyngobranchials II and III heavily toothed.

Color in preservative dark brown to black over entire surface of body (except for distal portion of escal bulb) and oral cavity; all fins colorless in specimens less than about 40 mm SL (except for caudal rays in adolescent *M. murrayi*, Bertelsen 1951, fig. 161).

Pectoral fin rays 15-23 (Table 2); pelvic fins absent.

The following measurements, in percent of standard length, are summarized for females (20-120 mm SL) of all species: head depth 42.5-82.0; least outside width between frontals 9.1-28.6; head width 22.6-45.0; premaxillary length 36.3-76.0; lower jaw length 36.7-78.0; width of pectoral fin lobe 6.1-17.8; escal bulb width 1.9-11.3

For description of males see Diagnosis above and Bertelsen (1951).

Genus *Melanocetus* Günther 1864

Females

Melanocetus Günther 1864:301-302, pl. 25 (type species *Melanocetus johnsoni* Günther 1864, by monotypy).

Melanocetus (subgenus *Liocetus*) Günther 1887:56, pl. 11, fig. A (type species *Melanocetus murrayi* Günther 1887, by monotypy).

Liocetus Goode and Bean 1896: 495-496, fig. 407 (type species *Melanocetus murrayi* Günther 1887, by monotypy).

Melanocoetus Smith 1949:429 (erroneous spelling of *Melanocetus*, therefore taking the same type species, *Melanocetus johnsoni* Günther 1864).

Linocetus Bertelsen 1951:40, 44 (erroneous spelling of *Liocetus*, therefore taking the same type species, *Melanocetus murrayi* Günther 1887).

Males

Rhynchoceratias Parr 1927:30-33, fig. 11-12 (in part; type species *Rhynchoceratias brevisrostris* Regan 1925, by subsequent designation of Fowler 1936).

Centroctetus Regan and Trewavas 1932:53, fig. 79 (type species *Centroctetus spinulosus* Regan and Trewavas 1932, by monotypy).

Xenoceratias Regan and Trewavas 1932:54-57, fig. 80-84 (type species *Xenoceratias longirostris* Regan and Trewavas 1932, by subsequent designation of Fowler 1936).

Diagnosis and description same as for family.

Key to Species Based on Females

The following key will differentiate female specimens >20 mm SL (for males and larvae see Bertelsen 1951). The key should be used in conjunction with Figures 19-24.

- 1A. Escal bulb width 11.3% SL in 111 mm specimen (Figures 18, 28); longest lower jaw tooth 5.9% SL in 111 mm specimen *Melanocetus eustalus* n. sp. (single known female)
- 1B. Escal bulb width <10% SL (Figure 17); longest lower jaw tooth 6.9-25.0% SL 2
- 2A. Anterior margin of vomer deeply concave (Figure 2); least outside width between frontals 9.1-17.8% SL (Figure 19); number of lower jaw teeth 46-142 (>60 in specimens 25 mm and larger) (Figure 20); escal bulb width 1.9-5.1% SL (<3% SL in specimens >50 mm SL) *Melanocetus murrayi* Günther 1887
- 2B. Anterior margin of vomer nearly straight (Figure 1); least outside width between frontals 13.5-28.6% SL (Figure 19); number of lower jaw teeth 32-90 (Figure 20); escal bulb width 3.8-8.6% SL (>4% SL in specimens >50 mm SL) 3
- 3A. Longest lower jaw tooth 8.4-25.0% SL (Figure 21); esca with compressed posterior and (usually) anterior crests (Figure 25); distribution nearly cosmopolitan
..... *Melanocetus johnsoni* Günther 1864
- 3B. Longest lower jaw tooth 6.9-13.1% SL (Figure 21); esca without posterior or anterior crests (Figures 26, 27); distribution restricted to eastern tropical Pacific 4
- 4A. Number of lower jaw teeth 58-90 (Figure 22); escal bulb width 5.2-8.5% SL (Figure 23); illicium length 34.6-56.0% SL (Figure 24); escal bulb with a conical, distal prolongation occasionally pigmented on tip (Figure 26) *Melanocetus polyactis* Regan 1925

4B. Number of lower jaw teeth 37-57 (Figure 22); esca bulb width 3.8-5.0% SL (Figure 23); illicium length 29.8-38.8% SL (Figure 24); esca bulb with a low, rounded distal prolongation usually darkly pigmented on tip (Figure 27) *Melanocetus niger* Regan 1925

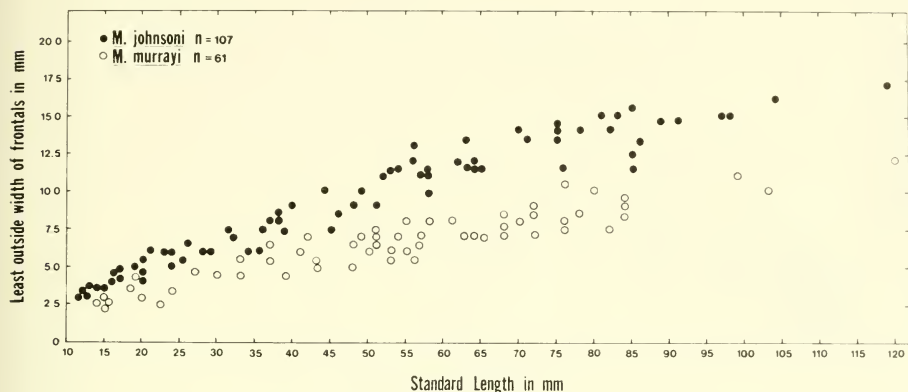


FIGURE 19.—Relationship between least outside width of frontals and standard length for two species of *Melanocetus*.

Melanocetus johnsoni Günther 1864

Figures 1, 3, 6, 16B, 17, 19-21, 25, 30, 31

Females

Melanocetus johnsoni Günther 1864:301-303, pl. 25 (original description, single specimen, holotype BMNH 1864.7.18.6, 64 mm, Madeira, 24 December 1863); Lütken 1871:64, 74 (comparison with *Oneiroides eschrichtii*); Lütken 1872:329-340, 343 (after Lütken 1871); Günther 1880:473, fig. 211 (after Günther 1864); Günther 1887:56-57 (after Günther 1864, comparison with *M. murrayi*); Vaillant 1888:346 (after Günther 1864); Goode and Bean 1896:494, fig. 406 (description after Günther 1864); Gill 1909:582, 584, 585, fig. 20 (after Günther 1864, Goode and Bean 1896); Regan 1912:286, fig. 6C (cranial osteology); Regan 1913:1096 (description of additional specimen, natural history); Regan 1926:18, 32, 33, fig. 10 (description of additional material, cranial osteology; *M. krechi* and *M. rotundatus* synonyms); Parr 1927:29 (description of additional specimen); Norman 1930:354 (additional record); Regan and Trewavas 1932:27-29, 49-52, fig. 19-21, 22A, B, 72, 73 (description of additional material, osteology, and esca figured, in key); Fowler

1936:1143, 1144, 1346, 1363 (description after Günther 1864, Regan 1926, Norman 1930); Norman 1939:114 (additional material); Koefoed 1944:3-5, pl. 1, fig. 1 (description of additional specimen, comparison with *M. murrayi*); Beebe and Crane 1947:152 (description of additional specimen, color); Fowler 1949:158-159 (listed); Bertelsen 1951:7, 40-41, 43-46, 48-53, fig. 13, 15, 17-19, tables 4, 6 (description of females, males, larvae, comparison with all known material, in key); Grey 1956:235-236 (synonymy; distribution); Monod 1960:687, fig. 80 (pectoral radials); Maul 1961:91-92, fig. 1 (description of additional material); Maul 1962a:6-7 (description, additional material); Struhsaker 1962:841-842 (description, additional specimen, skin spines); Bussing 1965:222 (additional specimen); Fitch and Lavenberg 1968:127, fig. 70 (distinguishing characters, natural history); Pietsch 1972a:29, 35, 36, 38, 45 (osteological comments); Maul 1973:667 (synonymy, after Bertelsen 1951).

Melanocetus krechi Brauer 1902:293-294 (original description, single specimen, holotype ZMHU 17688, 45 mm, *Valdivia* stn. 239, Indian Ocean, 5°42' S, 43°36' E, 0-2,500 m); Brauer 1906:319-320, pl. 15, fig. 1, 2 (description after Brauer 1902); Gill 1909:583, 584, fig. 21 (after Brauer

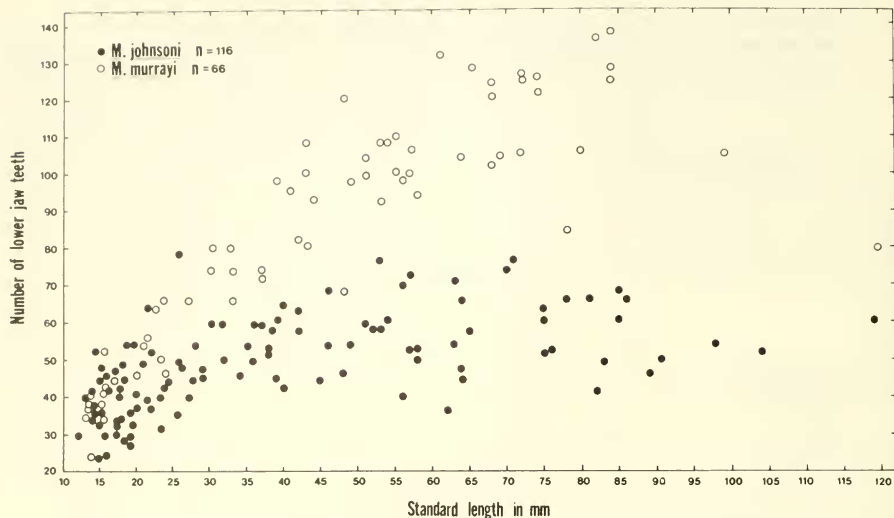


FIGURE 20.—Relationship between number of lower jaw teeth and standard length for two species of *Melanocetus*.

1902, 1906); Murray and Hjort 1912:87, 614 (in part, additional specimen, misidentification); Borodin 1931:84 (additional specimen, misidentification); Regan and Trewavas 1932:49, 52, fig. 74 (misidentification, in key); Fowler 1936: 1143, 1144 (description after Brauer 1902, 1906, in key); Bertelsen 1951:40, table 4 (comparison with all known material).

Melanocetus rotundatus Gilchrist 1903:206-208, pl. 15 (original description, two specimens, both lost [see Comments, p. 76], the largest about 28 mm, off Cape Point and Natal coast, South Africa, 1,098 m); Gilchrist and Thompson 1917:417 (after Gilchrist 1903); Barnard 1927:1007, pl. 37, fig. 5 (after Gilchrist 1903); Bertelsen 1951:48 (in synonymy of *M. johnsoni*).

Melanocoetus rotundatus, Smith 1949:429, fig. 1232 (after Gilchrist 1903); Penrith 1967:187, 188 (type material lost; a synonym of *M. johnsoni*).

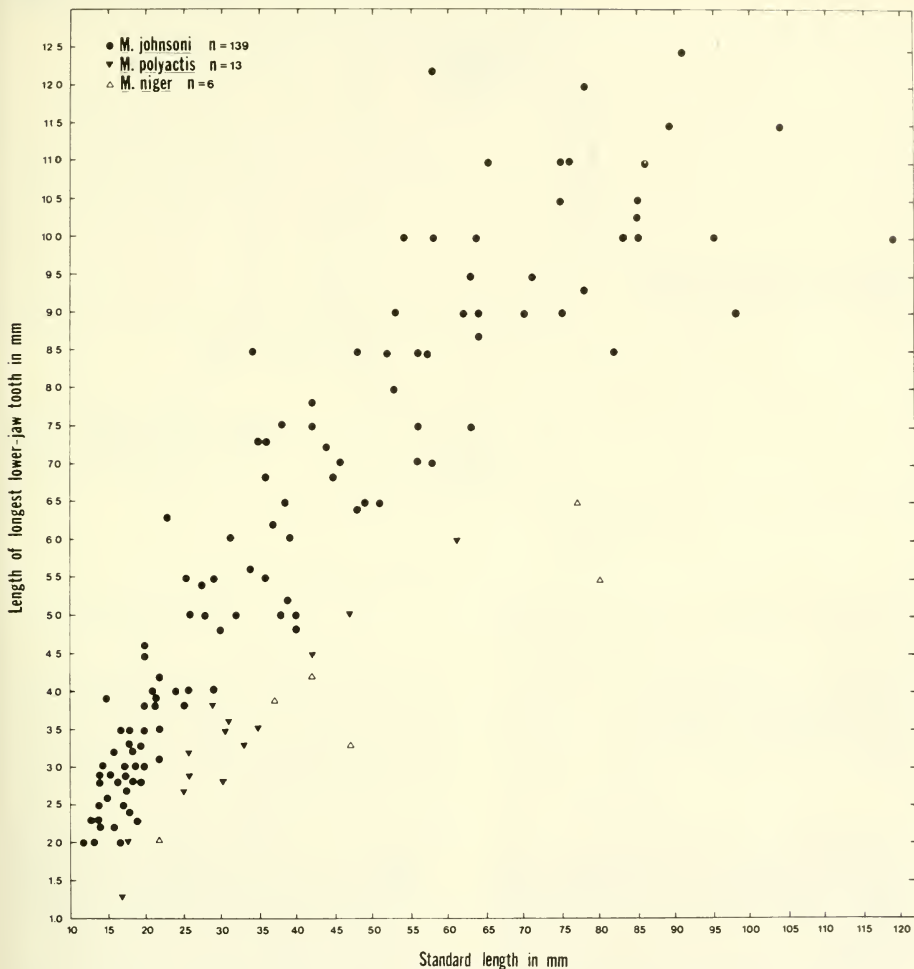
Melanocetus ferox Regan 1926:33, pl. 9, fig. 1 (original description, single specimen, holotype ZMUC P9257, 78 mm, *Dana* stn. 1208(14), Gulf of Panama, 6°48' N, 80°33' W, 3,100 m wire, 1715 h, 16 January 1922); Regan and Trewavas 1932:49, 52, fig. 75 (in part, only holotype, addi-

tional material here referred to *M. polyactis*, in key); Beebe and Crane 1947:152 (in part, only holotype); Bertelsen 1951:44, 53, table 4 (in part, only holotype; comparison with all known material, in key); Grey 1956:237 (synonymy, distribution).

Melanocetus cirrifer Regan and Trewavas 1932:52-53, fig. 76A, 77, pl. 2, fig. 1 (original description, two females, lectotype ZMUC P9258, 25.5 mm, *Dana* stn. 3678(2), Banda Sea, 4°05' S, 128°16' E, 4,000 m wire, bottom depth 4,700 m, 1840 h, 24 March 1929, in key); Bertelsen 1951:44, 53, table 4 (description, comparison with all known material, in key); Grey 1956:237 (synonymy, distribution).

Melanocetus niger, Gregory 1933:400, fig. 272 (misidentification, osteology).

Melanocetus megalodontis Beebe and Crane 1947:152, fig. 1 (original description, single specimen, holotype CAS-SU 46488 [originally NYZS 25791], 25.5 mm, Templeton Crocker Expedition stn. 165 T-3, eastern tropical Pacific, 20°36' N, 115°07' W, 0-915 m, 17 May 1936); Bertelsen 1951:43, 48, table 4 (description, comparison with all known material, in key); Grey 1956:235 (synonymy, distribution); Mead 1958:133 (holotype passed to CAS).


 FIGURE 21.—Relationship between length of longest lower jaw tooth and standard length for three species of *Melanocetus*.

Melanocetus sp. Roule and Angel 1930:121, pl. 6, fig. 159 (additional material).

Males

Centroctes spinulosus Regan and Trewavas 1932:53, 54, fig. 79 (original description, two specimens, lectotype ZMUC P9246, 15.5 mm,

Dana stn. 3847(2), Indian Ocean, 12°02' S, 96°43' E, 3,000 m wire, bottom depth 2,825 m, 2100 h, 11 October 1929).

Xenoceratias macracanthus Regan and Trewavas 1932:11, 12 (erroneous spelling of specific name, listed).

Xenoceratias micracanthus Regan and Trewavas 1932:54, 55, fig. 81 (original description, single

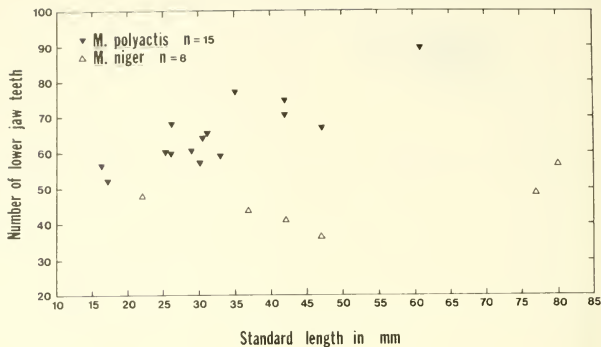


FIGURE 22.—Relationship between number of lower jaw teeth and standard length in two species of *Melanocetus*.

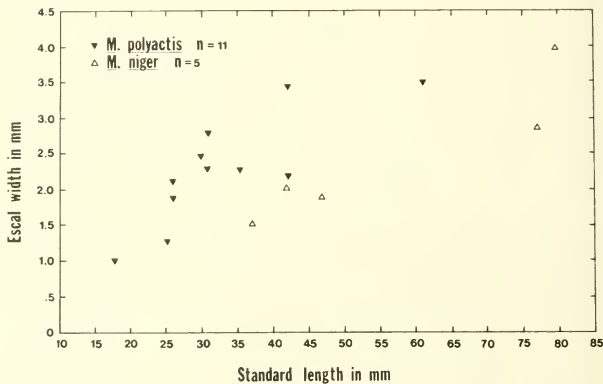


FIGURE 23.—Relationship between esca bulb width and standard length in two species of *Melanocetus*.

specimen, holotype ZMUC P9250, 28 mm, *Dana* stn. 4000(8), eastern tropical Atlantic, 0°31' S, 11°02' W, 4,000 m wire, bottom depth 3,750 m, 0630 h, 4 March 1930, in key); Fowler 1936:1364 (listed).

Xenoceratias heterorhynchus Regan and Trewavas 1932:54, 56, fig. 82 (original description, single specimen, holotype ZMUC P9248, 27 mm, *Dana* stn. 3716(2), South China Sea, 19°18.5' N, 120°13' E, 3,000 m wire, bottom depth 3,225 m, 1400 h, 22 May 1929, in key); Grey 1956:236 (synonymy, distribution).

Xenoceratias laevis Regan and Trewavas 1932:54, 57, fig. 83 (original description, single specimen, holotype ZMUC P9249, 23 mm, *Dana* stn. 3731(13), South China Sea, 14°37' N, 119°52' E, 2,000 m wire, bottom depth 2,300 m, 0200 h, 17 June 1929, in key).

Xenoceratias brevis Regan and Trewavas 1932:54, 57, fig. 84 (original description, single specimen, holotype ZMUC P9247, 19 mm, *Dana* stn. 3739(8), Celebes Sea, 3°20' N, 123°50' E, 3,000 m wire, bottom depth 4,475 m, 0700 h, 2 July 1929, in key).

Xenoceratias braueri Koefoed 1944:6, fig. 2 (original description, single specimen, holotype UBZM 4309, 18.5 mm, *Michael Sars* North Atlantic Deep-Sea Expedition stn. 53, central North Atlantic, 34°59' N, 33°01' W, 2,600 m wire, bottom depth 2,615-2,865 m, 8-9 June 1910).

Melanocetus johnsoni, Bertelsen 1951:44, 48-53, fig. 17C, D, F-H, table 6 (synonymy, distribution, comparison with all known material, in key); Grey 1956:236 (synonymy, distribution); Maul 1962b:36-37, fig. 2 (description of addi-

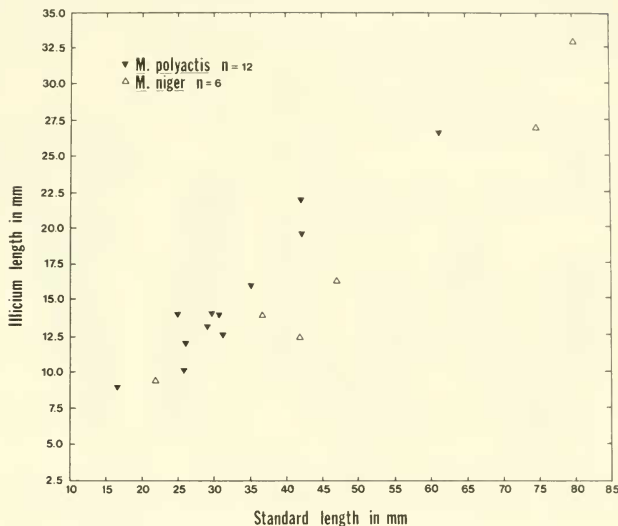


FIGURE 24.—Relationship between illicium length and standard length in two species of *Melanocetus*.

tional specimen); Maul 1973:667 (synonymy, after Bertelsen 1951).

Material. — Metamorphosed females, 346 (10-119 mm): AMS, 33 (11-88 mm); BMNH, 16 (13-64 mm); CAS, 1 (25.5 mm); FSM, 10 (13-76 mm); IOAN, 35 (12-75 mm); IOS, 7 (35-91 mm); ISH, 82 (15-119 mm); LACM, 65 (13.5-83 mm); MCZ, 25 (12-75 mm); NMNZ, 7 (12-55 mm); ROM, 4 (15-56 mm); SAM, 6 (10-13 mm); UMML, 3 (27-82 mm); USNM, 15 (12-85 mm); ZMUC, 37 (11.5-89 mm).

Diagnosis.—A species of *Melanocetus* unique in having the following combination of characters: anterior margin of vomer nearly straight (Figure 1); least outside width between frontals 13.5-28.6% SL (Figure 19); number of lower jaw teeth 32-78 (Figure 20), length of longest lower jaw tooth 8.4-25.0% SL (Figure 21); width of pectoral fin lobe 10.7-17.8% SL; esca bulb width 4.3-8.6% SL; illicium length 32.4-60.8% SL; esca with posterior and (usually) anterior crests (Figure 25); minute skin spines present over most of body; integument relatively thick (1.55 mm).

Description.—Esca bulb slightly compressed with a low, rounded or conical distal prolongation nearly always darkly pigmented on tip; a compressed posterior crest usually darkly pigmented,

becoming larger and more conspicuous with growth; and a considerably smaller, compressed, anterior crest present in some specimens (Figure 25); integument relatively thick (cross sections measure 1.55 mm in thickness), not easily torn, usually retaining heavy pigmentation during fixation and preservation.

Number of upper jaw teeth 48-134; dorsal fin rays 13-15 (rarely 16), pectoral fin rays 17-22 (rarely 23) (Table 2).

Distribution.—*Melanocetus johnsoni* has a wide horizontal distribution in tropical and subtropical waters of all three major oceans of the world (see Distribution, p. 83). Compared with *M. murrayi*, it appears to occupy relatively shallow depths: about 62% of the material (for which data was available) was captured by open nets fished at maximum depths of 1,000 m; 82% of the material can be accounted for by gear fished above 1,500 m, and 98% by gear fished above 2,100 m (see Distribution, p. 83).

Comments.—*Melanocetus krechii* Brauer (1902) was synonymized with *M. johnsoni* by Regan (1926), resurrected by Regan and Trewavas (1932), and tentatively synonymized again with *M. johnsoni* by Bertelsen (1951). From the description and figure given by Brauer (1902, 1906)

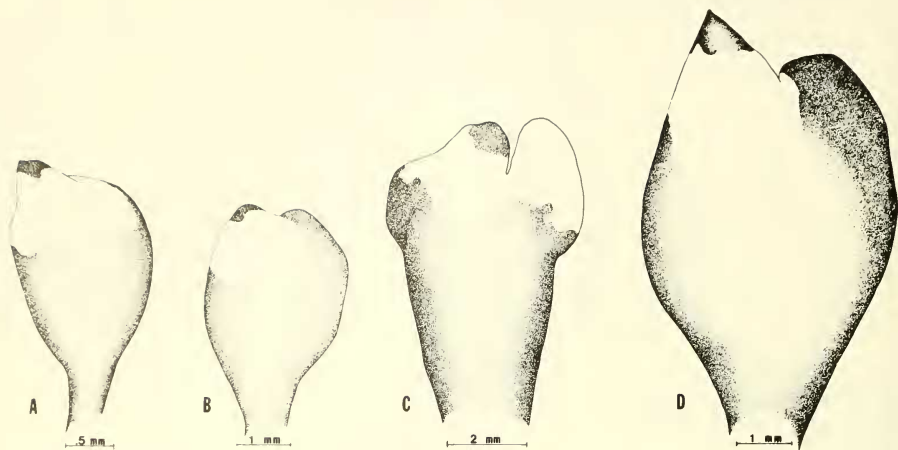


FIGURE 25.—Escae of *Melanocetus johnsoni*: A. ISH 1261/71, 21 mm SL; B. ISH 753/71, 38 mm SL; C. MCZ 49849, 75 mm SL; D. ISH 1534/71, 78 mm SL.

and based on a much greater knowledge of variation within the genus, there can be little doubt that this nominal form has been correctly placed within the synonymy of *M. johnsoni*.

Melanocetus ferox was described from a single specimen (78 mm) collected in the Gulf of Panama (Regan 1926). Two additional specimens of this nominal form were listed by Regan and Trewavas (1932). A thorough comparison of all known material led Bertelsen (1951, table 4) to suspect that *M. ferox* might represent individual variation of *M. niger*. The holotype of *M. ferox*, however, has relatively long lower jaw teeth (longest, 12.0% SL; Figure 21). In this, and in all other morphometric and meristic characters used here, it fits well within the material here recognized as *M. johnsoni*. Although the esca of the holotype is in poor condition, traces of a posterior crest remain. For these reasons *M. ferox* is synonymized with *M. johnsoni*. The two additional specimens identified as *M. ferox* by Regan and Trewavas (1932) (ZMUC P92210, 30.5 mm; BMNH 1932.5.3.6, 42 mm) have short jaw teeth; in this and in other ways they fit well within the material of *M. polyactis* (see p. 77).

Melanocetus cirrifer Regan and Trewavas (1932), described on the basis of two small females, was tentatively maintained by Bertelsen (1951) because of supposed differences in esca morphology and pigmentation which now can easily be

shown to be part of the variation found within *M. johnsoni*. *Melanocetus megalodontis* Beebe and Crane (1947), based on a single specimen, was distinguished from all other species of the genus by "... the character of the illicium; in the great length and robustness of the fangs ... and in the shortness of the lower jaw. ..." However, specimens of *M. johnsoni* may have longer teeth and individuals of several species of *Melanocetus* may have as short a lower jaw (Bertelsen 1951, table 4). Further (as predicted by Bertelsen 1951), the "peculiar minute distal flaps" of the esca are artifacts. In all ways the holotype of *M. megalodontis* fits well within the variation now known to occur within *M. johnsoni*. Thus these nominal forms, *M. cirrifer* and *M. megalodontis*, are placed within the synonymy of *M. johnsoni*.

Finally, the holotype and paratype of *M. rotundatus* Gilchrist (1903) have been lost. The circumstances of their demise are the same as for the holotype of *Dolopichthys cornutus* described elsewhere (Pietsch 1972b; see also Barnard 1927, Penrith 1967). Although Gilchrist's (1903) original description is poor, the figure provided by him shows rather long jaw teeth, a long illicium bearing a relatively large esca bulb, and a large pectoral fin lobe. This combination of characters makes it nearly certain that *M. rotundatus* is a synonym of *M. johnsoni* (Penrith 1967).

Melanocetus polyactis Regan 1925

Figures 21-24, 26, 30

Females

Melanocetus polyactis Regan 1925:565 (original description, 3 specimens, lectotype designated by Bertelsen 1951, ZMUC P9260, 61 mm, *Dana* stn. 1206(3), Gulf of Panama, 6°40' N, 80°47' W, 3,500 m wire, 1845 h, 14 January 1922); Regan 1926:34, pl. 8, fig. 2 (description after Regan 1925); Regan and Trewavas 1932:53, fig. 78 (listed, after Regan 1925, 1926); Bertelsen 1951:44, 54-55, tables 4, 7, 8 (description, additional material, 2 males, 6 larvae, comparison with all known material, in key); Grey 1956:238 (synonymy, distribution).

Melanocetus niger Regan 1925:565 (in part, 3 of 11 cotypes [see Comments, p. 79], all Gulf of Panama); Regan 1926:33, pl. 8, fig. 1 (in part, description, 4 additional specimens); Regan and Trewavas 1932:53, fig. 76B (in part, listed, after Regan 1925, 1926); Bertelsen 1951:44, 53, table 4 (in part, description, comparison with all known material, in key); Grey 1956:237 (in part, synonymy, distribution).

Melanocetus ferox, Regan and Trewavas 1932:49, 52, fig. 75 (in part, nontype material only, in key); Bertelsen 1951:44, 53, table 4 (in part, nontype material only, comparison with all known material, in key); Grey 1956:237 (in part, after Bertelsen 1951, synonymy, distribution).

Males

Rhynoceratias rostratus, Regan 1926:44 (in part, misidentification).

Rhynoceratias leucorhinus, Regan 1926:44 (in part, misidentification).

Material. — Metamorphosed females, 15 (16.5-61 mm): BMNH 1925.8.11.30, 26 mm; BMNH 1925.8.11.32, 42 mm (paralectotype); BMNH 1932.5.3.6, 42 mm; IOAN uncatalogued, 33 mm; LACM 33603-4, 2 (16.5 and 30 mm); LACM 33574-5, 17 mm; LACM 33624-1, 33 mm; LACM 33629-3, 35 mm; ZMUC P92155, 25 mm (paralectotype); ZMUC P921974, 26 mm; ZMUC P9251, 29 mm; ZMUC P92210, 30.5 mm; ZMUC P9253, 47 mm; ZMUC P9260, 61 mm (lectotype).

The following adolescent females, all collected from the eastern tropical Pacific, are only tenta-

tively referred to *M. polyactis*: LACM 33618-2, 16 mm; LACM 31119-2, 2 (17 and 18 mm); LACM 31109-2, 18 mm; LACM 31120-20, 2 (18 and 19 mm); LACM 31126-29, 2 (19.5 and 20 mm).

Metamorphosed males, 2: ZMUC P92460, 16 mm (22 mm total length (TL)); ZMUC P92459, 19.5 mm (30 mm TL).

Larvae, 6 (2 males, 4 females, 3-9 mm TL): ZMUC P92461; ZMUC P92462.

Diagnosis. — A species of *Melanocetus* unique in having the following combination of characters: anterior margin of vomer nearly straight; least outside width between frontals 18.0-26.0% SL; number of lower jaw teeth 58-90 (Figure 22); length of longest lower jaw tooth 9.3-13.1% SL (Figure 21); width of pectoral fin lobe 10.9-16.0% SL; escal bulb width 5.2-8.5% SL (Figure 23); illicium length 34.6-56.0% SL (Figure 24); esca with a conical, distal prolongation, crests absent (Figure 26); integument relatively thick.

Description. — Escal bulb not compressed, with conical distal prolongation nearly always slightly constricted at base, and usually as long as or longer than length of escal bulb, pigmented on tip in some specimens, posterior and anterior crests absent (Figure 26); integument as in *M. johnsoni*.

Number of upper jaw teeth 42-120; dorsal fin rays 14-17; pectoral fin rays 17-21 (rarely 22 and 23) (Table 2).

Distribution. — *Melanocetus polyactis* appears to be restricted to the eastern tropical Pacific Ocean where 15 specimens have been collected between lat. 10° N and 13° S as far west as long. 88° W (see Distribution, p. 83). Approximately 67% of the material was captured by open nets fished at maximum depths of 1,000 m or below.

Comments. — *Melanocetus polyactis* is most easily confused with *M. niger*. Both forms are similar in having exceptionally short lower jaw teeth (Figure 21). They differ significantly, however, in the number of lower jaw teeth, escal bulb width, and illicial length (see Key, Figures 22-24).

Part of the material originally listed as *M. niger* has been reallocated to *M. polyactis* (see Comments, p. 79). Also included with the material of *M. polyactis* are two specimens (ZMUC P92210, 30.5 mm; BMNH 1932.5.3.6, 42 mm) previously identified as *M. ferox* by Regan and Trewavas (1932).

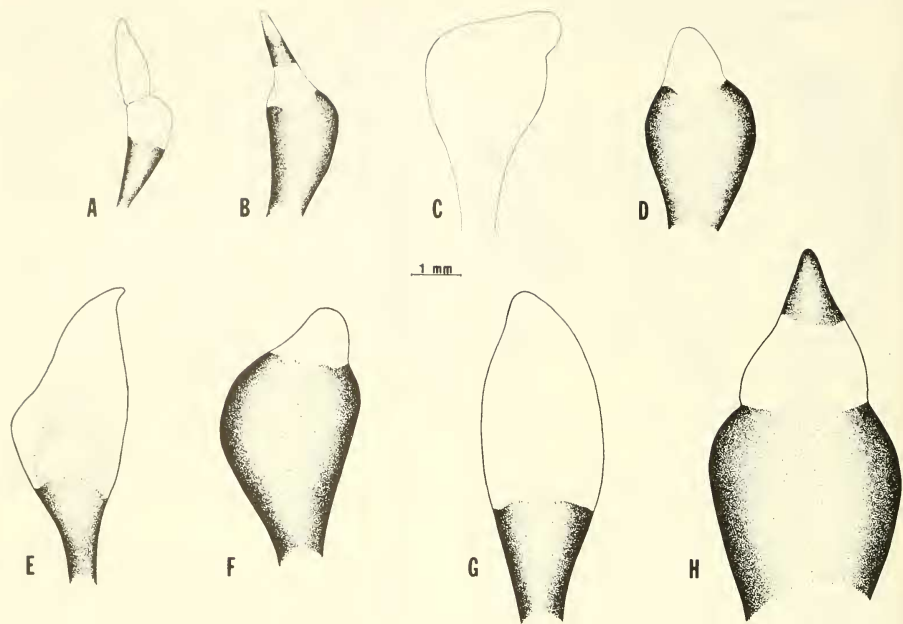


FIGURE 26.—Escae of *Melanocetus polyactis*: A. LACM 33603-4, 16.5 mm SL; B. Paralectotype, ZMUC P92155, 25 mm SL (lack of distal pigmentation probably due to abrasion); C. ZMUC P921974, 26 mm SL; D. ZMUC P9251, 29 mm SL (a cotype of *M. niger*); E. LACM 33603-4, 30 mm SL; F. ZMUC P92210, 30.5 mm SL; G. LACM 33629-3, 35 mm SL; H. Lectotype, ZMUC P9260, 61 mm SL.

Melanocetus niger Regan 1925

Figures 21-24, 27, 30

Melanocetus niger Regan 1925:565 (original description, in part, 4 of 11 cotypes [see Comments, p. 79] all Gulf of Panama, lectotype hereby designated, ZMUC P9252, 80 mm, *Dana* stn. 1208(4), 6°48' N, 80°33' W, 3,500 m wire, 0810 h, 16 January 1922); Regan 1926:33, pl. 8, fig. 1 (in part, description, 4 additional females); Regan and Trewavas 1932:53, fig. 76B (in part, listed after Regan 1925, 1926); Beebe and Crane 1947:153-154 (in part, description of 4 additional females not seen by us); Bertelsen 1951:44, 53, table 4 (in part, description, comparison with all known material, in key); Grey 1956:237 (in part, synonymy, distribution).

Material. — Metamorphosed females, 6 (22-80 mm): BMNH 1925.8.11.29, 47 mm (paralectotype); IOAN uncatalogued, 77 mm; ZMUC

P9254, 22 mm (paralectotype); ZMUC P9256, 37 mm (paralectotype); ZMUC P921973, 42 mm (*Galathea* stn. 727); ZMUC P9252, 80 mm (lectotype).

Males and larvae unknown.

Diagnosis. — A species of *Melanocetus* unique in having the following combination of characters: anterior margin of vomer nearly straight; least outside width between frontals 14.3-24.3% SL; number of lower jaw teeth 37-57 (Figure 22); longest lower jaw tooth 6.9-10.5% SL (Figure 21); width of pectoral fin lobe 9.1-13.5% SL; esca bulb width 3.8-5.0% SL (Figure 23); illicium length 29.8-38.8% SL (Figure 24); esca without crests (Figure 27); integument relatively thick.

Description. — Escal bulb not compressed, with a low, rounded or conical distal prolongation nearly always pigmented on tip; anterior and posterior

crests absent (Figure 27); integument as in *M. johnsoni*.

Number of upper jaw teeth 29-86; dorsal fin rays 14-15; pectoral fin rays 18-21 (Table 2).

Distribution. — All six known specimens of *M. niger* were collected in the Gulf of Panama and adjacent waters of the eastern tropical Pacific Ocean as far west as approximately long. 90° W (see Distribution, p. 83). Eighty-three percent of the material was captured by open nets fished at maximum depths of 1,500 m and below.

Comments. — *Melanocetus niger* was briefly described by Regan (1925) from seven specimens collected in the Gulf of Panama without type designation and without a listing of individual sizes, station numbers, or other means of identification. Regan (1926) added four more specimens without providing means of separating the original seven. All 11 specimens bear labels indicating cotype status and all are treated here as part of the original type material. One of these is designated the lectotype (ZMUC P9252, 80 mm), three are referred to *M. polyactis* (BMNH 1925.8.11.30, 26 mm; ZMUC P9251, 29 mm; ZMUC P9253, 47 mm), three unidentifiable specimens are listed below as *Melanocetus* sp. (ZMUC P9255, 13.5 mm; BMNH 1925.8.11.31, 14 mm; BMNH 1925.8.11.28, 43 mm), and one is unaccounted for and presumed lost (*Dana* stn. 1209(3), 37 mm total length). The

remaining three specimens are recognized as paralectotypes of *M. niger*.

Melanocetus eustalus n. sp.

Figures 18, 28, 30

Melanocetus ferox, Pietsch 1972b:10 (misidentification, luminescence); Brewer 1973:25 (after Pietsch 1972b, distribution).

Melanocetus sp. Pietsch 1976:782, 783 (reproduction).

Material. — A single female, the holotype, LACM 30037-12, 111 mm, *Velero IV* stn. 11748, eastern Pacific off Mazatlán, Sinaloa, Mexico, 21°39' N, 106°58' W, 3 m IKMT, 0-1,675 m, bottom depth 2,820 m, 1320-2136 h, 11 November 1967.

Diagnosis. — A species of *Melanocetus* unique in having the following combination of characters: anterior margin of vomer nearly straight; least outside width between frontals 18.0% SL; number of lower jaw teeth 60; longest lower jaw tooth 5.9% SL; illicium length 30.6% SL; width of pectoral fin lobe 9.9% SL; escal bulb width 11.3% SL; esca without crests (Figures 18, 28); integument relatively thick.

Description of holotype. — Escal bulb large (length 14.4% SL), slightly compressed, with a low conical distal prolongation, pigment absent; pos-

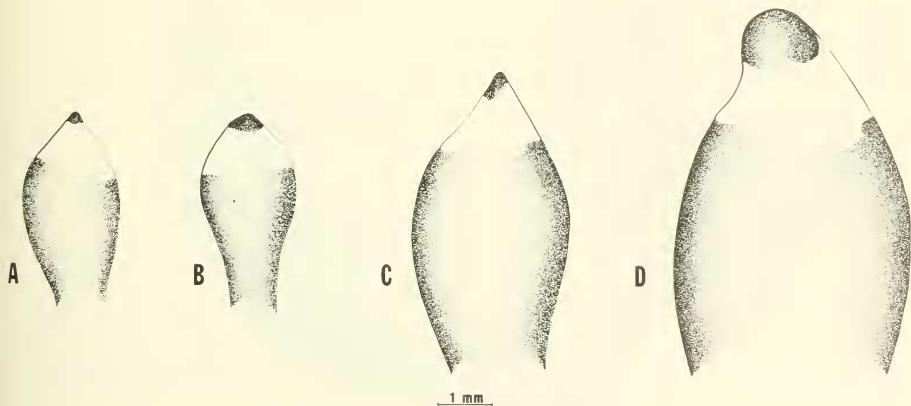


FIGURE 27.—Escae of *Melanocetus niger*: A. Paralectotype, ZMUC P9256, 37 mm SL; B. Paralectotype, BMNH 1925.8.11.29, 47 mm SL; IOAN uncatologued, 77 mm SL; D. Lectotype, ZMUC P9252, 80 mm SL.

terior and anterior crests absent (Figure 28); integument as in *M. johnsoni*.

Gill opening exceptionally large, greatest diameter 23.4% SL; number of upper jaw teeth 91; vomerine teeth 8; dorsal fin rays 15; pectoral fin rays 16 (Table 2).

Etymology. — The name *eustalus* is derived from the Greek *eustales*, an adjective meaning well

equipped, in reference to the enormous esca of this ceratioid.

Luminescence. — Upon capture, the holotype of *Melanocetus eustalus* was maintained alive for several minutes during which the bulb of the esca glowed continuously with a bright, golden-orange light. The amount of light actually emitted, however, appeared to be controlled by an up and down

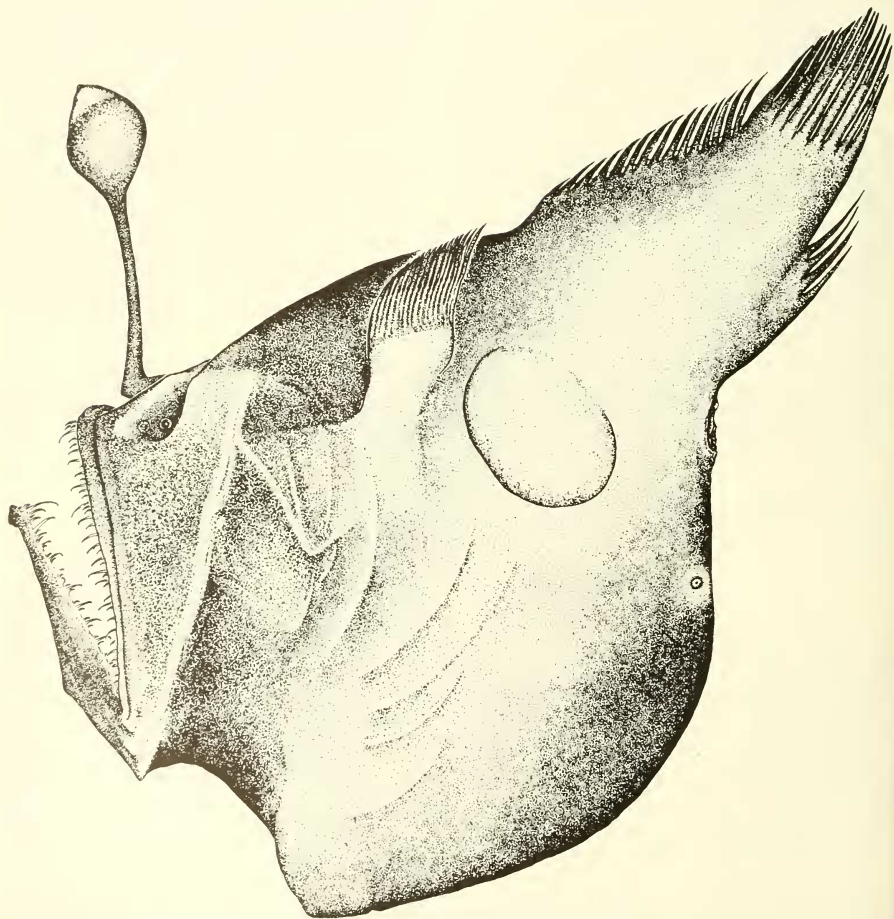


FIGURE 28.—Holotype of *Melanocetus eustalus*, LACM 30037-12, 111 mm SL, lateral view. Drawn by Elizabeth Anne Hoxie.

movement of the darkly pigmented, inner wall of the photophore of the esca. The glowing bulb was almost entirely covered and uncovered four or five times within a period of at least 1 min (B. G. Nafpaktitis³; see Pietsch 1972b). A mechanism of this kind would provide a rapid means of extinguishing light that may not only attract potential mates and prey, but also predators.

Melanocetus murrayi Günther 1887

Figures 2, 4, 5, 7-15,
16A, 19, 20, 29-31

Females

Melanocetus murrayi Günther 1887:57, pl. 11, fig.

A (original description, two specimens, lectotype BMNH 1887.12.7.17, 71 mm, *Challenger* stn. 106, central Atlantic, 1°47' N, 24°26' W, 0-3,386 m); Regan 1926:32 (description, additional material, in key); Parr 1927:27 (description, additional material); Regan and Trewavas 1932:27, 49-50, fig. 22C, 23, 71 (description, additional material; pectoral radials, pelvic bone, escae figured; in key); Beebe 1932:99-102, fig. 29, 30 (description of postlarvae); Parr 1934:7 (listed); Fowler 1936:1143, 1144-1145, 1346, 1363, fig. 483 (after Günther 1887; Regan 1926; in key); Koefoed 1944:3, 5 (description, comparison, additional material); Fowler 1949:158 (listed); Bertelsen 1951:40-48, fig. 16, tables 4, 5 (description of females, males, larvae, comparison with all known material, in key); Grey 1955:299 (additional material, color); Grey 1956:234 (synonymy; distribution); Monod 1960:687, fig. 80 (pectoral radials); Pietsch 1972a:34, 38 (osteological comments); Maul 1973:667 (synonymy, after Bertelsen 1951).

Melanocetus bispinosus Günther 1880:473 (name only); Goode and Bean 1896:495 (in synonymy).

Melanocetus (Liocetus) murrayi Günther 1887:56 (original description, a distinct subgenus).

Liocetus murrayi, Goode and Bean 1896:495, fig. 407 (new combination, after Günther 1887); Gill 1909:583, 584, fig. 22 (after Günther 1887; Goode and Bean 1896).

Melanocetus vorax Brauer 1902:294 (original description, single specimen, holotype ZMHU 17710, 85 mm, *Valdivia* stn. 63, Gulf of Guinea,

2°00' N, 8°04' W, 0-2,492 m); Brauer 1906:320-321, pl. 15, fig. 4 (description after Brauer 1902). Fowler 1936:1143, 1144 (description after Brauer 1902, 1906; in key).

Melanocetus johnsoni, Brauer 1906:319 (misidentification); Regan 1926:33 (in part, misidentification); Murray and Hjort 1912:609, 614, 618, fig. 469 (misidentification); Fowler 1936, fig. 482 (figure after Brauer 1906).

Melanocetus krechi, Murray and Hjort 1912:614, 618 (in part, misidentification).

Melanocetus tumidus Parr 1927:28-29, fig. 10 (original description, single juvenile, holotype BOC 2022, 15 mm, *Pawnee* Third Oceanographic Expedition stn. 11, western North Atlantic, 23°58' N, 77°26' W, 2,135 m wire, 2 March 1927); Regan and Trewavas 1932:49 (mentioned); Grey 1956:239 (synonymy, distribution, a young female *M. murrayi*).

Melanocetus niger, Parr 1927:29 (misidentification); Beebe 1929:18 (misidentification).

Males

Rhynchoceratias acanthiostriis Parr 1927:31, fig. 11 (original description, single specimen, holotype BOC 2011, 20 mm, *Pawnee* Third Oceanographic Expedition stn. 22, western North Atlantic, 23°37' N, 77°15' W, 2,135 m wire, 12 March 1927); Parr 1930b:130, 134 (anatomy, life history).

Rhynchoceratias latirhinus Parr 1927:32, 33, fig. 12 (original description, single specimen, holotype BOC 2012, 15 mm, *Pawnee* Third Oceanographic Expedition stn. 33, western North Atlantic, 24°11' N, 75°37' W, 2,440 m wire, 22 March 1927).

Rhynchoceratias longipinnis Parr 1930a:7, fig. 2-5 (original description, single specimen, holotype BOC 2592, 16 mm, *Pawnee* Third Oceanographic Expedition stn. 59, Bermuda, 32°19' N, 64°32' W, 2,440 m wire, 21 April 1927, osteology); Parr 1930b:129, fig. 1-3, 6, 7 (anatomy, life history).

Xenoceratias acanthiostriis, Regan and Trewavas 1932:54, 55 (new combination; description after Parr 1927, in key).

Xenoceratias longipinnis, Regan and Trewavas 1932:54, 56 (new combination; description after Parr 1927, in key).

Xenoceratias latirhinus, Regan and Trewavas 1932:54, 57 (new combination; description after Parr 1927, in key).

³B. G. Nafpaktitis, Professor, Department of Biological Sciences, University of Southern California, Los Angeles, CA 90007, pers. commun. November 1967.

Xenoceratias regani Koefoed 1944:4, 6, pl. 1, fig. 6 (original description, single specimen, holotype UBNM 4311, 20 mm, *Michael Sars* North Atlantic Deep-Sea Expedition stn. 53, central North Atlantic, 34°59' N, 33°01' W, 2,600 m wire, bottom depth 2,615-2,865 m, 8-9 June 1910).

Melanocetus murrayi, Bertelsen 1951:44-48, fig. 16A, D, F, H, table 5 (synonymy, description, comparison with all known material, in key); Grey 1956:235 (synonymy, distribution); Maul 1962b:37-38, fig. 3 (description of additional specimen); Maul 1973:667 (synonymy, after Bertelsen 1951).

Material. — Metamorphosed females, 140 (13.5-120 mm): BMNH, 8 (21-57 mm); BOC, 1 (15 mm); CAS, 3 (14.5-51 mm); FSM, 6 (13.5-54 mm); IOAN, 5 (14-56 mm); IOS, 6 (17-68 mm); ISH, 33 (15-120 mm); LACM, 14 (13-84 mm); MCZ, 14 (13-84 mm); UMML, 28 (17-99 mm); USNM, 7 (15-78 mm); VIMS, 1 (33 mm); ZMUC, 14 (14-80 mm).

Diagnosis. — A species of *Melanocetus* unique in having the following combination of characters: anterior margin of vomer deeply concave (Figure 2); least outside width between frontals 9.1-17.8% SL (Figure 19); number of lower jaw teeth 46-142 (Figure 20); longest lower jaw tooth 7.7-16.7% SL; width of pectoral fin lobe 6.1-8.9% SL; escal bulb width 1.9-5.1% SL; illicium length 23.1-37.2% SL;

esca with crests minute or absent (Figure 29); minute skin spines restricted to caudal peduncle; integument relatively thin (0.48 mm).

Description. — Escal bulb not compressed, with a low, rounded distal prolongation usually unpigmented on tip; posterior and anterior crests minute or absent (Figure 29); integument thin, easily torn (cross sections measure 0.48 mm in thickness), pigment readily lost during fixation and preservation, often transparent, especially in gill region and over branchiostegal rays.

Number of upper jaw teeth 34-178; dorsal fin rays 12-14, pectoral fin rays 15-19 (rarely 20) (Table 2).

Distribution. — *Melanocetus murrayi* has a wide horizontal distribution in the Atlantic and Pacific, but is apparently absent from the Indian Ocean (see Distribution, p. 83). Compared with *M. johnsoni*, it is a much deeper living form: only 10% of the material (for which data was available) was captured in open nets fished at maximum depths of <1,000 m. Approximately 58% of the material was taken by gear fished at maximum depths of 1,500 m or below, and 45% by gear fished at 2,000 m or below (see Distribution, p. 83). The relatively thin integument of *M. murrayi* (less than one-third the thickness of that of its congeners) as well as a lighter, less well-ossified skeleton reflects the poorer trophic economies of these greater depths (see Description above).

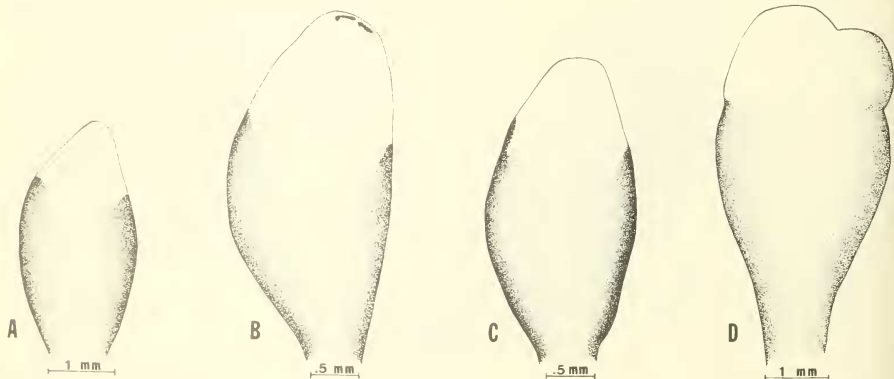


FIGURE 29. — Escae of *Melanocetus murrayi*: A. ISH 2961/71, 58 mm SL; B. ISH 922/68, 70 mm SL; C. ISH 2961/71, 76 mm SL; D. ISH 2961/71, 120 mm SL.

Comments.—*Melanocetus vorax* Brauer (1902) was tentatively synonymized with *M. murrayi* by Regan (1926). This decision was confirmed by Regan and Trewavas (1932) and later by Bertelsen (1951). *Melanocetus tumidus* Parr 1927 (not mentioned by Bertelsen 1951) was based on a single metamorphosing female (15 mm) that fits well within the larval and metamorphosing material of *M. murrayi* (Bertelsen 1951) in lacking pigment on the caudal peduncle and having a faintly pigmented gill cover. This nominal form is hereby synonymized with *M. murrayi*.

Species Incertae Sedis

The following two nominal species based on males are distinguished from other *Melanocetus* males in having the posterior nostril well separated from the eye. They are probably not specifically distinct from each other and are most likely the males of one of the above recognized species based on females (Bertelsen 1951, fig. 20).

Melanocetus longirostris (Regan and Trewavas 1932) Incertae Sedis

Xenoceratias longirostris Regan and Trewavas 1932:54, 55, fig. 80 (original description, single specimen, holotype ZMUC P9259, 21 mm, *Dana* stn. 3751(7), north of New Guinea, 3°40' N, 137°53' E, 3,000 m wire, 1240 h, 12 July 1929); Fowler 1936:1346 (after Regan and Trewavas 1932; type species designation).

Melanocetus longirostris, Bertelsen 1951:42-44, 54 (new combination, comparison with all known material, in key); Grey 1956:238 (synonymy, distribution after Bertelsen 1951).

Melanocetus nudus (Beebe and Crane 1947) Incertae Sedis

Xenoceratias nudus Beebe and Crane 1947:155, text fig. 2 (original description, single specimen, holotype CAS-SU 46495 [originally NYZS 28402], 21.5 mm, Eastern Pacific *Zaca* Expedition stn. 210T-8, south of Cape Blanco, Costa Rica, 9°12' N, 85°10' W, 915 m, 27 February 1938).

Melanocetus nudus Bertelsen 1951:43-44, 54, fig. 20 (new combination, description of one additional specimen, comparison with all known material, in key); Grey 1956:238 (synonymy, distribution after Bertelsen 1951).

Melanocetus species

The following females, all considered to be part of the original type material of *M. niger* (see Comments, p. 79), are so poorly preserved that they cannot be referred to any described species of the genus: BMNH 1925.8.11.31, 14 mm; ZMUC P9255, 13.5 mm; BMNH 1925.8.11.28, 43 mm (illicium absent).

The following males cannot be satisfactorily identified to species based on females. Variation in the number of denticular teeth and pectoral fin rays and in the subdermal pigmentation (Bertelsen 1951) is considerably greater than previously thought (see Diagnosis of family above): LACM, 73 (11.5-24 mm) (66 from Hawaii at lat. 21°20'-30' N, long. 158°20'-30' W; 3 from the Banda Sea; 2 from the Mid-American Trench at approximately lat. 18° N, long. 104° W; and 2 from the Equator at about long. 170° E and 145° W).

DISTRIBUTION

The family Melanocetidae is widely distributed throughout all three major oceans of the world in a broad belt limited by the Arctic and Antarctic Polar Fronts, with northern and southernmost records at approximately lat. 62° N and 46° S. It is present in the Gulf of Mexico, but has not been collected in the Gulf of California or the Mediterranean Sea (Figure 30).

Two of the five species of the family are wide ranging forms: *M. johnsoni* occurs throughout the Atlantic, Pacific, and Indian Oceans; *M. murrayi* is found throughout the Atlantic and Pacific Oceans but has so far not been recorded from the Indian Ocean. Two lesser known species, *M. polyactis* and *M. niger*, are restricted to the eastern tropical Pacific Ocean. *Melanocetus eustalus* is represented by a single specimen collected in the eastern Pacific off Mazatlán, Sinaloa, Mexico.

Since the majority of collections of melanocetids were made with nonclosing nets, the actual depth of capture is unknown. Furthermore, because sample sizes are small a statistical treatment of the nonclosing net data is impossible. Assuming, however, that most specimens were caught at depths where gear is fished for the longest period of time, vertical distributions may be roughly estimated by referring to the maximum depth reached by gear for each capture. On this assumption, members of the Melanocetidae may be taken anywhere between 250 m and some unknown

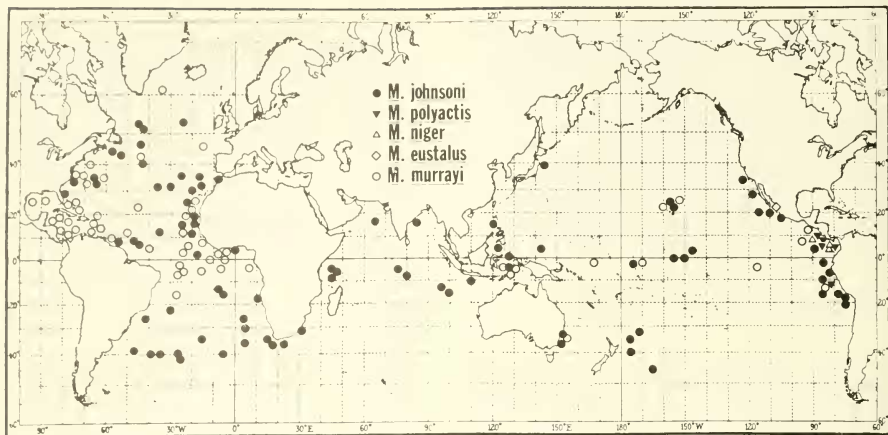


FIGURE 30.—Geographical distribution of *Melanocetus* species. Symbols may indicate more than one capture.

lower depth limit exceeding 3,000 m, but they are commonly found between roughly 500 and 2,500 m. *Melanocetus johnsoni* is most often collected between 500 and 1,500 m. *Melanocetus murrayi* is a considerably deeper dwelling species; the bulk of the known material was collected between 1,000 and 2,500 m (Figure 31). The relatively thin integument (see Description above) and lighter, less well-ossified skeleton of *M. murrayi* reflects the poorer trophic economies of these greater depths. The remaining species of the genus are so poorly represented in collections that their vertical distributions cannot be estimated.

EVOLUTIONARY RELATIONSHIPS

The Melanocetidae appears to be a relatively underived ceratioid family (Bertelsen 1951; Pietsch 1972a, 1976, 1979). The five species are characterized by a confusing mosaic of primitive and derived character states such that an interpretation of interspecific phylogenetic relationships is difficult. In any case, however, it seems apparent that *M. murrayi* has split off from the main line of melanocetid evolution and acquired a number of unique features that reflect its most derived position in the genus: 1) depressed cranium, 2) concave vomer, 3) small pectoral fin, 4) tiny esca bulb, and 5) thin integument. Living in considerably deeper strata than its congeners most probably also reflects a derived condition.

The four remaining species are much more closely related to each other than any is to *M. murrayi*. Five characters can be used to distinguish these forms: 1) number of lower jaw teeth, 2) longest lower jaw tooth, 3) illicium length, 4) esca bulb width, and 5) esca morphology. Unfortunately, all but the last of these characters overlap in variation among the remaining forms of the genus, and, furthermore, the relative primitiveness of character states among these features is nearly impossible to determine. *Melanocetus johnsoni* is perhaps derived in having a relatively long illicium, and in having fewer, but longer jaw teeth (see Pietsch 1972b, 1974, 1975). *Melanocetus polyactis* and *M. niger* are similar in having relatively short jaw teeth, a similar esca morphology lacking anterior and posterior crests, and a sympatric geographic distribution that is restricted to the Gulf of Panama and adjacent eastern tropical Pacific. *Melanocetus eustalus* is derived in having an extremely large esca bulb, comparable with no other known ceratioid.

ACKNOWLEDGMENTS

We thank E. Bertelsen for critically reading the manuscript and offering valuable suggestions. The following people and institutions provided study material: John R. Paxton (AMS), Alwyne Wheeler (BMNH), William N. Eschmeyer (CAS), Carter Gilbert (FSM), N. V. Parin (IOAN), Nigel

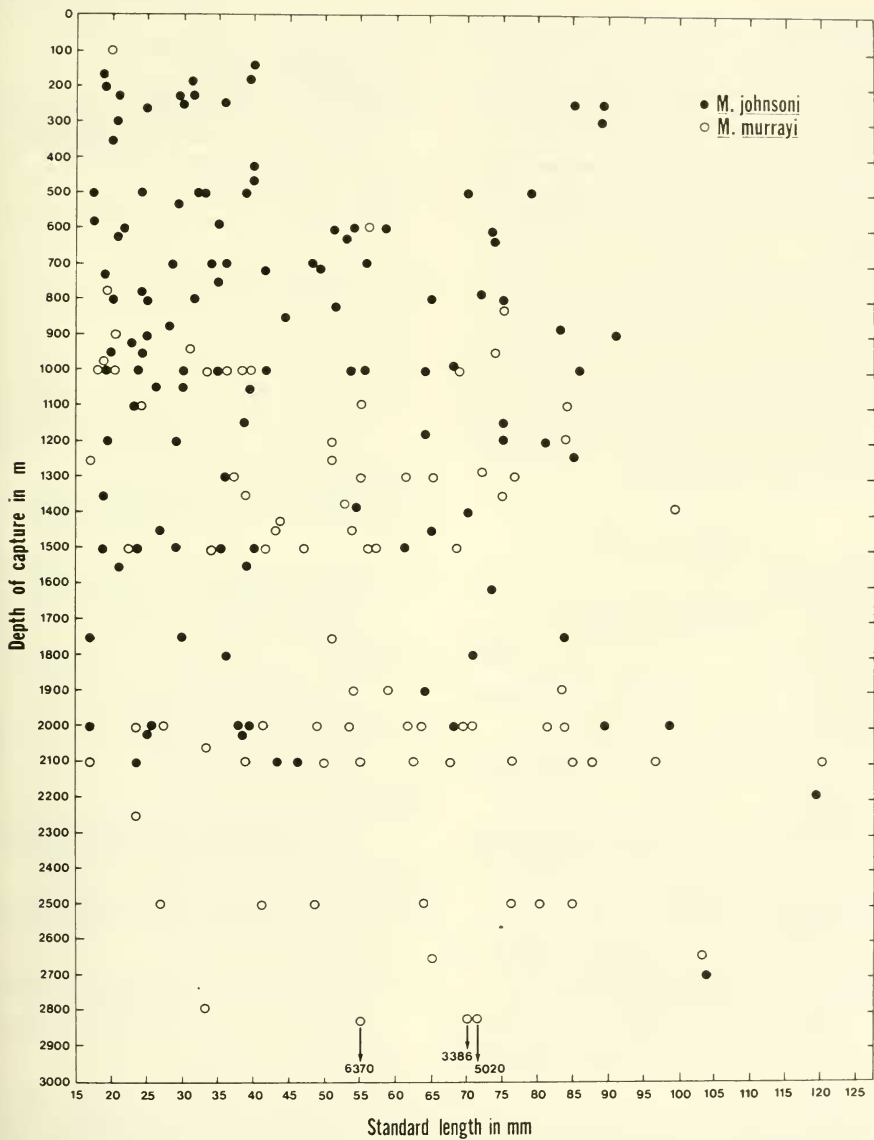


FIGURE 31.—Relationship between depth of capture (based on maximum depth reached by fishing gear) and standard length for two species of *Melanocetus*.

Merrett (IOS), Gerhard Krefft and Alfred Post (ISH), Robert J. Lavenberg and Jerry W. Neumann (LACM), Karsten Hartel (MCZ), Jack Moreland and C. D. Paulin (NMNZ), Allen Emery (ROM), P. A. Hulley (SAM), C. Richard Robins (UMML), Robert H. Gibbs and Susan Karnella (USNM), E. Bertelsen (ZMUC), Thomas A. Clarke (Hawaii Institute of Marine Biology), Richard E. Young (University of Hawaii at Manoa), Brett Stephenson (Auckland Museum, New Zealand), and Don A. Robertson (Ministry of Agriculture and Fisheries, Wellington, New Zealand). Elizabeth Anne Hoxie provided Figures 17, 18, and 28. The work was supported by National Science Foundation Grants GB-40700, DEB 76-82279 and DEB 7826540, the National Geographic Society, and PHS Biomedical Research Support Grant No. RR-07096 administered through the Graduate School Research Fund of the University of Washington.

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